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INHERITANCE OF SOME MORPHOLOGICAL  
CHARACTERS IN *CREPIS CAPILLARIS*\*

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INTRODUCTION

Geneticists studying the inheritance of characters in plants have been following with interest the monumental investigations on *Drosophila* by Morgan and others, with especial attention to their studies on the inheritance of both qualitative and quantitative characters. The present paper reports the result of an investigation on the inheritance of some quantitative characters in a wild plant, *Crepis capillaris* (L.) Wallr. The studies included characters in leaves and flowers, and it will be shown that the inheritance of these characters is similar to the inheritance of quantitative characters in other organisms.

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## OBJECTS AND AIMS

The genus *Crepis*, comprising over 150 species, belongs to the tribe Cichorieae of the natural order Compositae, and is closely related to the genus *Hieracium*. The species, *C. capillaris*, so far as known, has not been brought under cultivation, but grows as a wild plant in widely separated parts of the world. This species can be easily propagated and the plants are self-fertile so that investigations may be carried on with inbred strains. Furthermore, the  $F_1$  and  $F_2$  generations from varietal crosses are fertile when crossed *inter se*, and the species has a very low number of chromosomes. Hence as Babcock (1920) pointed out, the advantages of the genus for genetic investigation are many. Previous to that, some work had been done on the cytological side, notably by Rosenberg (1909-1918), who determined the number of chromosomes, Beer (1912), Miss Digby (1914) and de Smet (1914). De Smet has given excellent illustrations of the various stages of nuclear division. Other species of *Crepis* have been studied by Rosenberg (1909-1918) and Juel (1905); interspecific crosses between *C. capillaris* and *C. tectorum* have been reported by Babcock and Collins (1920). The achenes of *C. capillaris* germinate easily after a short period of rest and a very large percentage is viable. The plant first develops a rosette and finally the central axis elongates and terminates in an inflorescence; but under unfavorable conditions it may remain indefinitely in the rosette stage. The plant is strictly annual, however, and dies after once flowering. Plate 43 illustrates typical plants when the inflorescence has developed and growth has practically ended.

The present investigation has to do specifically with differences in the length of the radical leaves, in the number of lobes on the radical leaves, and in the diameter of the flower heads. The aim was to determine whether these differences were inherited and to locate the factors responsible for the genetic variations as distinct from modifications due to the environment. In the case of the inheritance of morphological characters in the leaf, the action of the environment had to be taken into consideration, and in the case of the flowers, the action of the environment in addition to the age of the plant and the position of the capitulum upon the plant had to be evaluated before the true genetic variations could be determined. The work has been carried on

partly in the greenhouse and partly in the field and the results have been found so consistent that the data have been combined. The investigations herein reported were started in the fall of 1920 and were carried on by the writer until July, 1922, but a great deal of preliminary purification of material had been done before the material was turned over to me.

The work was undertaken at the suggestion of Professor E. B. Babcock, head of the Division of Genetics, University of California, to whom my best thanks are due. My thanks are also due to Dr. R. E. Clausen and Mr. J. L. Collins, of the Division of Genetics, for especially valuable help and suggestions during the progress of the investigations.

## MATERIAL AND METHODS

The detailed work has been done on three inbred families. The achenes were always germinated in seed pans in which the soil had been sterilized, or which had been filled with soil near which no *Crepis* plants had been grown within the last few years. The achenes were lightly covered with soil and watered. The germination was fairly rapid and the seedlings were ready for transplantation in about four weeks from the date of sowing. They were transferred either to small cardboard boxes about two inches square and planted out in the field or to 4-inch or 6-inch pots directly. The size of the pot had very little influence on the early development of the plant although, so far as general vigor was concerned, the plants in the 6-inch pots gave better results.

In measuring the length of the leaves and determining their lobe number, the plants were allowed to develop as far as possible in the rosette stage and data were secured before the central axis appeared with the formation of the cauline leaves. The length of the leaf was measured on a centimeter scale and the number of lobes counted on one side of the leaf, usually the left side. Every lobe which was supplied with a distinct vein was given a unit rank and in these calculations all scurs at the base of the leaf and the secondary lobes attached to the main ones were not considered. Five leaves were indiscriminately chosen and counts made upon them.

The capitula were measured on the centimeter scale when they were fully open. Flower heads in *Crepis* open centripetally, and a

flower head was considered fully open when all the disc florets had opened and the stigmas were projecting. This stage is usually maintained for two or three days. Then the capitula widen and spread out, and measurements taken at this stage always give results which are about 3 mm. more than the actual diameter when the heads are fully open. Moreover the flowers open at about 9 a.m. on bright days and remain open till after 3 p.m. if the day is not hot. But on dull and cloudy days they open about 10 a.m. or later, and occasionally they fail to open altogether. The 25 flowers first formed were measured in every case and their individual measurements noted. Inflorescence in *Crepis* closely follows the type described by Gleason (1919) for *Vernonia mussurica*. The main axis is the first to give off flowers, and the few branches at the top are more or less leafless. The flowers form a more or less flattened corymb at the top. The lower nodes bear shorter and frequently less developed lateral branches which usually appear so late in the season that none of the heads, or only a part of them, open their flowers and set seed before the plant has exhausted itself and dies down. In *Vernonia* three types of variations were investigated: (1) a variation between the heads of each cyme, possibly correlated with their position whether terminal or inferior; (2) a variation between different floriferous branches of the same plant possibly correlated with the amount of available nourishment; (3) a general variation between different individuals, possibly correlated with the size and vigor of the plant and therefore indirectly with the habitat. Gleason finds that within a single cyme of from two to six heads the terminal head is the largest. In larger cymes, some of the secondary terminal heads are frequently larger than the primary terminal head, the number of flowers is greatest for the terminal head of each cyme, but it is relatively constant for each individual plant. Two sets of factors, which may be environmental, or hereditary, or both, are involved. One determines the number of heads produced and the other the average number of flowers in each head. These act upon the plant independently and thus give four classes: many large heads, many small heads, few large heads, and few small heads. This investigator based his measurements and conclusion on 25 flowers. Goodspeed and Clausen (1915) estimate 25 as the minimum number on which to base any calculations for flower size. Goodspeed and Clausen (1918) have described a mechanical apparatus by which measurement of flowers is made. East uses only a millimeter scale; I have followed East in this work.



With regard to the method of cross-pollinating the plants, both the methods suggested by Babcock and Collins (1920) were tried, and depollination with a water jet has given results as good as emasculation, although the latter method was employed in all cases of critical investigation. The flowers were enclosed in translucent paper bags to prevent insect pollination and the achenes gathered before they were over-ripe and dropped to the ground or were taken off by the wind. It is fairly easy to decide whether a cross-pollination has been successful or not because the involucre assumes an ovoid form in the successful crosses, whereas it remains more or less oblong in the unsuccessful ones. The achenes, moreover, are plump and the ribs marked, the seed coat itself being distinctly colored as compared with that of the unfertilized achenes.

#### INHERITANCE OF LENGTH OF LEAF

In *Crepis capillaris* the first true leaves are small (about twice the size of the cotyledons), and there is a continuous increase in leaf size until the rosette is formed. Plate 42 shows stages of growth of the leaves including the mature rosette when they are ready for measuring. Even in the early stages the plants show different habits of growth, some growing erect and others spreading horizontally. In one family especially (20.6) there is a tendency for the leaf margins to curl downward, thus rendering measurement difficult (plate 42, fig. 4). In the earlier work, the leaves were clipped off with a pair of fine scissors close to the stem and measured on a centimeter ruler. But later on it was thought that injuring the plants thus might affect the result, and the leaves were kept intact on the plant while the ruler was thrust in as close to the stem as possible. Five mature leaves were measured at random and the average of the readings has been taken to represent the mean length of leaf in the plant. In table 1 it will be seen that the length of leaf fluctuates widely from the mean as compared with the breadth. The variation in length was 12.6 to 23.0 cm. in family 20.1, 11.8 to 18.4 cm. in family 20.6, 15.8 to 30.7 cm. in family 20.11 and from 24.0 to 40.1 cm. in family 20.13. Crosses were made between the 20.1 family with a range from 13 to 23 cm., and family 20.13 with a spread of 21.0 to 40.1 cm. with a view to studying the way in which the factors for length segregated. Table 2 gives the usual biometrical data for the various families studied. This table indicates that the factors for length show segregation in  $F_2$ , but owing to the fact that the environment plays such a great part in

determining the length, it is difficult to estimate the number of factors involved. (See Hayes, 1912, p. 34.) Figure 1 shows the length of leaves typical of the parent races, and typical leaves from the  $F_1$  population. Figure 2 shows typical leaves from plants of the  $F_2$  generation. The drawings have been made from actual prints of leaves on photographic paper and reduced equally in reproduction.

TABLE 1  
SHOWING MEASUREMENTS OF LENGTH AND WIDTH OF LEAVES

20.1		20.6		20.11		20.13	
Length cm.	Width cm.	Length cm.	Width cm.	Length cm.	Width cm.	Length cm.	Width cm.
22.2	3.9	18.1	4.5	15.8	3.1	29.4	4.0
17.3	3.6	15.5	4.3	23.3	4.4	34.0	5.0
17.2	3.5	14.6	3.7	25.5	6.8	35.0	6.0
15.0	2.5	16.3	3.5	30.7	6.8	30.0	3.6
18.4	2.8	11.8	2.0	20.0	4.5	40.1	5.8
15.5	3.4	16.1	3.7	29.5	7.3	26.1	5.1
15.6	3.4	16.0	3.7	32.2	5.6	37.7	6.5
15.6	3.4	14.7	3.2	28.6	6.0	26.0	3.5
20.0	3.4	18.4	4.5	18.5	5.0	24.0	3.0
23.0	4.4	13.2	2.5	28.6	6.0	28.0	6.0
19.8	2.9	14.9	3.6			33.0	4.5
12.6	2.0	15.8	3.1			34.0	6.0
						24.0	3.5
						34.0	5.6
						29.0	5.0
						31.0	4.0
						31.5	3.8
						23.0	3.0
						31.0	5.0
						21.0	2.5
						21.6	3.0
						29.5	4.3
Total: 212.2	35.8	185.4	42.3	252.7	55.5	652.9	98.7
Average: 17.7	3.0	15.45	3.5	25.3	5.5	29.7	4.5

It should be stated that the plants of the  $F_2$  population were grown in 4-inch pots while those of the parent races and  $F_1$  population were in 6-inch pots. However, the  $F_2$  plants were all grown under uniform conditions so that the evidence of segregation in both leaf length and number of lobes may be referred to genetic differences among the  $F_2$  plants.

## INHERITANCE OF THE NUMBER OF LOBES

The problem of the number of lobes on the leaves resolves itself into four distinct subheads. The first of these involves the question whether the leaf shall be considered lobed at all. There are families in which the lobing, if present, is so shallow that the leaves would be described as entire or merely dentate. This type is designated as

TABLE 2  
SHOWING THE RESULTS OF CROSSING FOR INHERITANCE OF LEAF LENGTH

Nature of Cross	Generation	Mean	Stand. deviation	Coef. of Var.
20.1 x 20.13	P <sub>1</sub>	17.9 ± .588	2.89 ± .468	16.1
	P <sub>1</sub>	29.7 ± .699	4.97 ± .495	16.7
	F <sub>1</sub>	29.0 ± .282	2.33 ± .188	8.0
	F <sub>2</sub>	14.9 ± .137	5.28 ± .097	35.4

Applying Castle's formula

$$n = \frac{(29.7 - 17.9)^2}{8(5.28^2 - 2.33^2)} = \frac{139.24}{179.2}$$

Factors responsible for length = 1 factor.

This result is very improbable, but the results can be interpreted on a modified dihybrid ratio of 9:6:1 where the two single homozygous genotypes give identical effects. On this ratio and from a study of the data, the result may be stated thus:

A B = 9, leaf length from 6 — 18 cm.

A b = 3, leaf length from 19 — 25 cm.

a B = 3, leaf length from 19 — 25 cm.

a b = 1, leaf length from 26 — 34 cm.

Where factors A and B stand for two independent factors in the absence of both of which the double recessive a b is obtained:

Observed numbers: 491 : 158 : 27

Calculated numbers: 378 : 252 : 42.

simplex in the accompanying account. There is another type where the lobes are distinct and simple and look like the steps on a ladder. This is designated as the scalaris type. A third type has a complex type of lobes where the scalaris type of lobing is surmounted by smaller secondary lobules or wings. The second subhead refers to the incision or depth of lobing. In the families studied the lobing extended halfway from the margin to the mid-rib or completely to the mid-rib. The third subhead concerns number of lobes on the leaf and the fourth refers to the character which is shown when the secondary lobules instead of remaining attached to the main lobes are

separated and form independent lobes attached to the mid-ribs. The first of these is the major character because, without a tendency to form the lobes, the rest of the factors could not express themselves. But the remaining three subheads behave as separate groups of factors, the depth of incision having an independent action on the leaf as do the other two characters mentioned above. One thing, however, was clear from the studies made, and that was the complex way in which

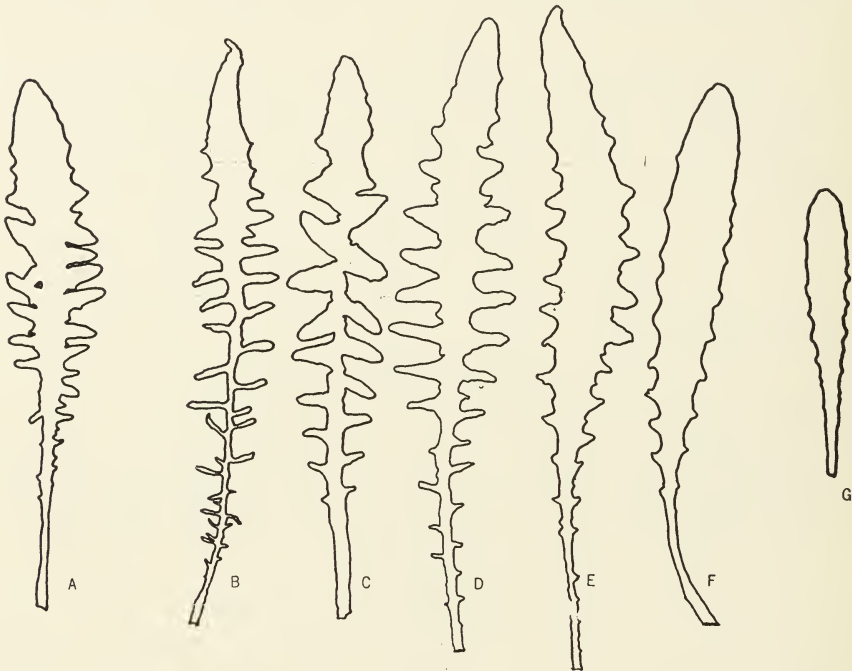


Fig. 1a. A typical leaf of the race with long leaves and many lobes. *g.* A typical leaf of the race with short leaves and few lobes. *b-f.* Typical leaves from different plants of the  $F_1$  generation. *c.*  $\times \frac{1}{3}$ .

each of these characters was inherited. That these groups of characters are inherited in a Mendelian fashion cannot be doubted, but the work has not advanced enough to estimate with certainty the number of factors involved in these cases, except in the number of lobes, which has been more extensively studied.

The same families that furnished material for studying the inheritance of length have been used for studying the lobe numbers. Table 3 shows the lobe numbers of the various families handled in this work. The same illustrations, figures 1 and 2, show the nature of lobing and the number of lobes.



TABLE 3  
SHOWING THE RESULTS OF CROSSING FOR INHERITANCE OF NUMBER OF LOBES

Nature of Cross	Generation	Mean	Stand. deviation	Coef. of Var.
20.1 x 20.13	P <sub>1</sub>	8.9 ± .352	1.73 ± .248	19.4
	P <sub>1</sub>	11.3 ± .171	1.21 ± .134	10.7
	F <sub>1</sub>	11.17 ± .156	1.37 ± .110	12.2
	F <sub>2</sub>	8.1 ± .087	3.36 ± .061	41.5

Applying Castle's formula the number of factors would be

$$\frac{(11.3 - 8.9)^2}{8(3.36^2 - 1.37^2)} = \frac{5.76}{75.2}$$

an obvious impossibility.

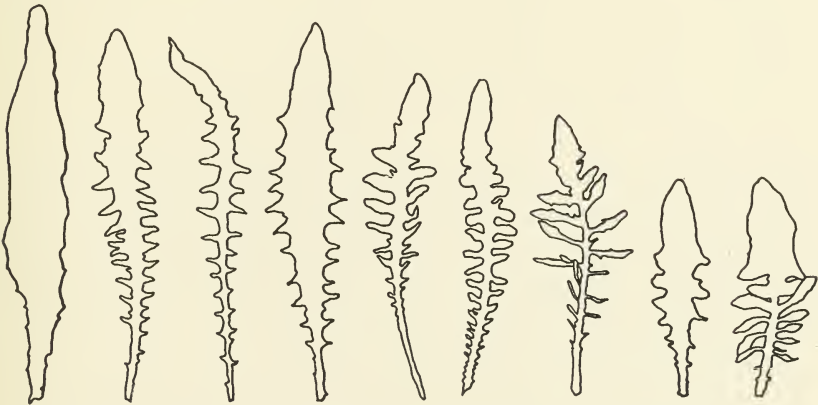


Fig. 2.—Typical leaves from different plants of the F<sub>2</sub> generation. c. × 1/3.

The data can be interpreted on a four factor hypothesis where each factor in a homozygous condition contributes two lobes and, in a heterozygous condition, one lobe. On this hypothesis the genotypic formula would be,

a	a	b	b	c	c	d	d	5
a	a	b	B	c	c	d	d	6
a	a	B	B	c	c	d	d	7
a	A	B	B	c	c	d	d	8
A	A	B	B	c	c	d	d	9
A	A	B	B	C	c	d	d	10
A	A	B	B	C	C	d	d	11
A	A	B	B	C	C	D	d	12
A	A	B	B	C	C	D	D	13

and the data on this hypothesis would give a curve which simulates the normal curve of error with the mode at 8.

From the data presented in table 3, it is fair to conclude that there is segregation with respect to mean lobe number in  $F_2$ . Both the  $F_1$  and  $F_2$  are intermediate between the two grandparent types and in the latter there is no transgressive segregation on the side of the higher number of lobes. The number of lobes ranges from 6 to 13 in the  $F_2$  family 21.141 and arranging the plants in class groups their distribution is as follows, the mean being at 9.

6	31
7	42
8	54
9	35
10	47
11	37
12	9
13	1

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256

This tabulation shows that the inheritance of lobe number is complicated; and, while more of the plants show the lobe number of the lower numbered parent, the majority of them are intermediate as required by the hypothesis of multiple factors. The same remarks apply to the other  $F_2$  populations studied, and there must be at least four factors responsible for number of lobes in the leaves.

The length of the leaf has little or no influence upon the number of lobes in the leaves. The accompanying correlation chart, table 4,

TABLE 4  
CORRELATION TABLE FOR NUMBER OF LOBES (x) AND LENGTH OF LEAF IN CM. (y)  
FAMILY 21.140

	4	5	6	7	$\Sigma y$
8-11	....	10	4	....	14
11-14	1	15	25	....	41
14-17	....	11	17	1	29
17-20	....	8	46	6	60
20-23	....	9	54	4	67
23-26	....	9	38	1	48
26-29	....	4	8	0	12
$\Sigma x$	1	66	192	12	

$$r_{xy} = 0.2302 \pm 0.0388$$

constructed for family 21.140, shows that the correlation between the two is very low. For purposes of calculation, length of lobe is expressed in round numbers of centimeters, the fraction being treated as one when more than half and ignored when less than that amount.

The absence of influence of length of leaf on number of lobes is also illustrated by a comparison of the leaf outlines which show practically the same number of lobes on leaves of different lengths and in other cases different numbers of lobes on leaves of practically the same length. From an extended study of the data as well as from observations in the field and green house on various races of *Crepis capillaris*, I am led to conclude that number of lobes is a definitely heritable character and is not influenced by length of leaf, by soil or by any other environmental conditions under which the plant is grown.

#### INHERITANCE OF SIZE OF CAPITULUM

Goodspeed and Clausen (1915) have determined a number of factors which influence flower size in *Nicotiana*. Under the heading, "age of plant," they have considered the difference in size of flowers borne early in the season as compared with those borne late in the season on the same plants as well as the difference in size of flowers during the first blooming season of the plant compared with that of flowers produced the next year and on the same plants cut back and sprouting from the roots. Under the heading "age of flower," they include, first, a consideration of the difference in the size of flowers borne on the terminal inflorescences first coming out of the stem and those borne at the same time on laterals and seconds, and (2), the influence of age on the individual flower by comparing measurements of flowers fully opened before and after shedding pollen. Other factors such as influence of removal of flowers and developing seed capsules, the behavior of cuttings under various conditions, and the influence of soil fertility were also studied. They find that the flowers produced later in the season have usually been of smaller size. By removing all flowers as fast as they are produced, they find it possible to keep the flower size nearly equal to that of the first flowers produced and were able in some cases to double the length of a plant's life. During the period which elapses from the time a flower is fully opened to the time when pollen is shed, there is a considerable increase in corolla spread, and associated with it, little or no increase in corolla

length. Soil also had a great influence in their experiments in determining the size of the flowers. "The conclusion seems irresistible that flower size in *Nicotiana* is not so constant as it has been assumed to be, but that it is affected by a number of conditions and that at least some of these may not affect the length and spread in the same manner."

#### INFLUENCE OF AGE OF PLANT

In *Crepis capillaris*, the 25 capitula first formed are usually very uniform and show a very narrow range of variation. The terminal flower is usually the largest, although the next two flowers below it are of the same size in many instances; but usually there is a significant difference of 1 mm. when a large number of flowers are measured. The flowers were pulled off and measured in every instance, which eliminated to a large extent the possibility of the flowers' growing slightly smaller. As a rule the 25 flowers required were measured in about a week's time, although the plant normally continues to flower for about four to five weeks. Flowers measured at the end of a season are about 15 to 20 per cent smaller than those measured at the beginning and, owing to the setting of seed and senility of the plant, all the buds formed do not open. In an experiment which was carried on to measure the entire lot of flowers that were produced on 6 plants of a strain, the plants started flowering on the tenth of February and continued till the end of April. Comparing the early flowers with those formed later, the size of the latter is smaller. But this reduction is not so great as in the case of plants from which no flowers are removed. Two things can be noted, however, in the flowers formed later. The number of flower heads that open on any given day is less than before and the number of florets per head is significantly smaller, the capitulum showing a more open center. The actual size of the floret is not perceptibly reduced and this accounts for the fact that the size of the flowers remains fairly constant. Another character that can be seen in the flower heads formed later is the slender elongated stalks on which they are borne as compared with the robust stalks of the earlier formed flower heads, while in many cases the internodes between the flower stalks are longer in the later formed flowers.





the inflorescence and furnishes the measurements of the diameters of individual capitula of a single plant. Comparing the individual cymose clusters, the terminal cluster has the largest central flower: closely followed by the next few lower clusters. As the measurements are followed farther down, the central capitulum becomes slightly smaller. The lateral capitula are generally smaller than the central capitulum in each cluster, but at times they may attain to the same size, especially in the uppermost cymes. Very rarely they are larger than the central capitulum of the cyme of which they are laterals. The central capitula of the lower cymes may be larger than the lateral capitula of the upper cymes. In comparing flower heads as to size, however, the facts that all the capitula do not ripen at the same time and that the age of the plant is a factor causing variation should be kept in mind. Moreover, in this group of measurements, the flowers were pulled off for measuring, and this has a tendency to keep the inflorescence active for a longer time and to maintain the flower size, as has been noted by Goodspeed and Clausen. The facts as to variation of size in the flowers, due to the age and position of the flower, may be summarized by saying that, in plants allowed to flower normally, the terminal flower head is usually the largest, closely followed by the second and third flower heads, after which the size becomes slightly smaller. The relative size of the flowers on the lower branches is similar, but the terminal flowers on the lower branches are smaller than the terminal flower of the whole plant or than those terminal flowers which arise from branches in the axils of the uppermost leaves.

#### ENVIRONMENTAL FACTORS

*Light.*—With regard to the effect of light on the flowering of plants, some interesting results have been obtained. Klebs (1918) in his work on *Sempervivum* divided the process of flower formation into three distinct stages: (1) production of the condition of ripeness to flower, (2) formation of flower primordia, and (3) development of flower clusters and elongation of the axis. He found that light is the dominant factor in determining all three stages. More recently Garner and Allard (1920) have published their opinion that the three primary factors that enter into the action of light upon plants are (1) intensity of the light, (2) quality, that is, the wave length of the

radiation, and (3) duration of exposure. They conclude that the relative length of day is a factor of prime importance in the growth and development of plants, particularly with respect to sexual reproduction, and in 1922 they confirmed and amplified their work. I have been able to confirm this work to a certain extent. A culture of plants growing in the greenhouse was close to an electric lamp used to maintain a constant temperature in a chamber close by, and the plants that were closest to this lamp flowered first, the arc of flowering spreading out centrifugally. After some time all the plants that were near the lamp had flowered, although the rest of the cultures took nearly two months longer to produce flowers. Moreover, the plants that bloomed first were in a comparatively disadvantageous position during the day, so that the effect of the artificial illumination on the flowering of the plants is all the more striking. This observation was repeated in an attempt to hasten the process of flower formation. Two strains of plants, 0215 and 0217, which were both  $F_1$  progeny of crosses made by me, were growing very slowly and were still in the rosette stage by the end of March of this year due to the cold winter. In order to hasten their growth and obtain seed for growing an  $F_2$  population, a few of them were placed three feet below a 300 Watt electric lamp surrounded by a reflector every day from 6 p.m. to 8 a.m. the next day. Some of them shot out flower buds in about three weeks from the time the experiment was started. The rest of the plants in the same families which were not subjected to artificial light had in many cases not started to send up the central floriferous axils. The heat from the lamp may also have had a slight effect.

*Moisture.*—The plants as they grow in pots in the greenhouse are not subject to much variation in soil moisture because they are watered regularly and the minimum soil moisture necessary for proper growth is usually maintained. The case of the plants grown in the field, however, was different because irrigation water was applied periodically, and owing to the variation in temperature of the days intervening between two successive irrigations, the soil moisture was neither constant, nor was it always above the minimum water requirements of the plants. Consequently, the flowers gradually got smaller as time elapsed after irrigation until, during the hottest part of the day, the plants would show signs of withering. Measurements were taken at this period and showed comparatively the smallest size in the diameter of the capitula. This difference went up usually

to a maximum of 4 mm., but usually it ranged between 2 mm. and 3 mm., and more often reached the lower limit. If at this stage the land was irrigated, the measurements taken the next day invariably showed a rise. The following data taken on plants of the same population both before and after irrigation illustrate this point.

—Culture Hsu 20.1—

Number of plant	Before Irrigation		After Irrigation	
	Number of flowers measured	Average diameter in cm.	Number of flowers measured	Average diameter in cm.
3	4	1.87	5	2.16
9	4	1.97	5	2.22
27	4	1.90	6	2.10
38	3	2.00	5	2.22
49	3	1.96	4	2.25
59	5	1.98	4	2.05
77	4	2.05	5	2.16
99	3	2.00	5	2.16
Total	30	1.95	39	2.16

There is an average difference of 0.21 cm. or approximately 2 mm.

#### A CROSS INVOLVING DIFFERENCE IN HEAD SIZE

This particular work was started in the summer of 1921 and was carried only to the  $F_1$  stage. Two strains were chosen, one having a diameter ranging from 17 to 25 mm., and the other from 21 to 36 mm. These races had undergone a preliminary purification for size of flower head. The  $F_1$  was intermediate and the mean of the  $F_1$  population was closer to the mean of the smaller parent than that of the larger parent. The data that have been secured on this work are given in table 5. Other crosses have given similar results, but as the parent strains did not differ in any marked degree, the  $F_1$  obtained shows about the same size of head diameter.

TABLE 5  
SHOWING RESULTS OF CROSSING FOR DIAMETER OF CAPITULUM

Diam. of heads in mm.	Frequencies		
	H21.1	B21.13	F <sub>1</sub> hybrids
17	8		
18	74		
19	266		17
20	444		42
21	343	19	85
22	368	53	98
23	278	60	142
24	149	33	103
25	71	36	94
26	24	16	32
27		29	12
28		25	
29		7	
30		10	
31		12	
32		11	
33		13	
34		2	
35			
36		1	
Mean	21.27 ± .027	25.37 ± .131	22.96 ± .048
Stand. Dev.	1.84 ± .019	3.52 ± .093	1.81 ± .036
Coef. Var.	8.6	13.87	7.8

## DISCUSSION OF RESULTS

1. The leaves of *Crepis capillaris* vary in outline from a simplex through a scalaris to a bipinnate type of lobing. In the first case, as evidenced by one of the parents used in the cross (fig. 1) the outline is more or less entire, while the other parent in this cross represents the scalaris type. The F<sub>1</sub> progeny obtained exhibited considerable variation but were always intermediate between the two extreme types. In the F<sub>2</sub> there was decided segregation and since only one plant out of over 250 showed characters almost similar to one grandparent, there must be more than one factor responsible for the occurrence of lobes as well as for the number of lobes. The cross 20.1 × 20.13 has

given an intermediate number of lobes in  $F_1$  generation and in  $F_2$  the progeny ranged from one parent type to the other. Out of the 250  $F_2$  plants studied not one fully represented the grandparent types, and on mathematical considerations there must be at least four factors responsible for this condition. Shull (1918) in his work on the leaf forms of the Shepherd's Purse has formulated a two factor hypothesis, the double dominant homozygote, the two single dominant homozygotes and the double recessive, giving the four classes which he obtained. With regard to the work on the length of the leaf, it has been found that, as compared to the length, the breadth of a leaf is a much more constant character as shown by table 6. The data for this table were

TABLE 6

SHOWING AVERAGE LENGTH AND WIDTH OF LEAVES IN 100 PLANTS OF FAMILY 20.140

Length in cm.	17	18	19	20	21	22	23	24	25	26	27	28
Number of plants	2	6	10	6	6	10	15	13	11	13	6	2

Width in cm.	2.0	2.2	2.4	2.6	2.8	3.0	3.2	3.4	3.6
Number of plants	13	11	26	27	8	9	0	5	1

obtained from a family of plants selected at random. This observation is in accordance with the reports of some other investigators. Moreover, the length of a leaf is more markedly susceptible to environmental influences and fluctuations due to modifications will profoundly interfere with estimating the effects of recombinations. It is therefore believed that races should be purified for the breadth factor rather than for the length factors for facilitating studies in this direction.

During the progress of the work, several crosses were made between strains of *Crepis*, and some of the strains were inbred. The result in many cases was comparable to the results of inbreeding in corn. As Collins (1920) has noted, plants of inbred strains may not put out flowers at all, or if they do, very few of the heads set seed. Some of these are viable and give rise to seedlings which may not thrive very well unless they are given special care. They are not as strong as those obtained from hybrid plants. When they have grown beyond the seedling stage, they sometimes stay in the rosette stage much longer than is usual and the vegetative period is consequently prolonged. One strain remained in the rosette stage and produced no flowers although it had been growing for over a year and a half. Other abnormalities have also been noted, such as vegetative proliferation and fasciation of stems and peduncles. Often the flower heads are fasciated and



flattened on two sides assuming the shape of an oval as opposed to the normal round shape and at times, owing to a shortening of the pedicels, two or three flowers appear to be joined together. All these malformations have been noted in one or another of the cultures, and emphasize strongly the effects of inbreeding in bringing to light undesirable recessive characters which are disadvantageous to the growth of the individual plant.

The outcome of this portion of the work has given results in no way contradictory to the conclusions arrived at by other investigators who have relied upon multiple factors as an explanation of inheritance of quantitative characters. As the experiment has not been carried to the  $F_3$  stage, it is not possible to state whether this material will yield results entirely consistent with the requirements (East, 1916) of the multiple factor hypothesis. But as far as the results go, they are in agreement with the explanation suggested that inheritance of the number of lobes in *Crepis capillaris* is a Mendelizing quantitative character and that it is controlled by many factors which affect occurrence of lobes, depth of the incisions, number of lobes, and shape of the lobes.

It may be here noted, in passing, that in a work of this nature a certain amount of discretion is necessary in determining the class to which a given individual belongs. Classification of the shape of a leaf and the exact number of its lobes are, to a certain extent, decided by the investigator, who can handle them quickly as he gains practice. Moreover, the exact times when the measurements are to be taken are more or less fixed by the investigator himself, who should try to secure as uniform material as possible in the several generations. East (1921) has raised a similar point in his work as regards the personality of the investigator. He says, "I believe that in such work as this, the investigator who lives with his plants in the field, who uses all the quantitative data at his command, but who, nevertheless, brings to his aid all the somewhat intangible facts that intimate experience gives him is able to come to a better realization of the truth than one who works on cold data obtained by others."

2. Size of capitulum is a character which is controlled by genetic factors, and it is fairly constant for a given family. It is practically independent of the size of the plant and it cannot fall below a certain minimum. It is also independent of the number of capitula on the entire plant or the number of florets per flower head. It is similarly uninfluenced by the shape of the plant. The tall, erect, vertical type of plants, and the bushy spreading type of plants (pl. 43) have given

sizes of flowers which are practically identical (see East, 1921, p. 329) and while casual observation leads me to believe that the number of flowers per plant and the number of florets per head vary directly with the size and shape of the plant, the diameter of the flower head is not subject to influence by any one of these three factors and is relatively stable. (See Stout, 1918.) The only factor that has been found to influence the size of the flower heads is the moisture content of the soil. The drier the soil the smaller the heads become. Here the plants in pots have an advantage because the soil is never allowed to become dry and the slight variations of moisture to which the plants in pots are subject do not affect the diameter of the flower heads to any appreciable extent. The results obtained from field plants are strictly comparable among themselves, however, since all the strains are subject to the same unfavorable environmental influences and as such give results strictly comparable.

### SUMMARY AND CONCLUSIONS

1. *Crepis capillaris* has been found to be a valuable species for genetic investigations because it is a wild plant which has not been subjected to conscious selection by human agency.

2. It can be cross-fertilized and the progeny derived from such cross-fertilization is fertile *inter se* and gives viable seed.

3. Several characters in the plant are constant and breed true when the material has been purified to bring it into a homozygous condition for the character in question.

4. Continual selfing of the plant is followed by the usual symptoms of such treatment in naturally cross-fertilized species, resulting in reduced vitality, arrested development at the rosette stage, formation of many sterile flowers, few viable achenes, vegetative proliferation and fasciation of the capitula and the stem.

5. Three quantitative characters were studied in this plant: the length of the leaf, the number of lobes in the leaves, and the diameter of the flower heads.

6. Length of leaf is a heritable character, but the environment has a very great influence. The resulting fluctuating variability is so great that although crosses have been made for studying the type of inheritance, it is difficult to classify and segregate the  $F_2$  progeny.

7. In inheritance studies, width of leaf is a better index of leaf size than length.

8. Number of lobes per leaf is constant for any given race of plants and the character is determined by four sets of factors:

- (a) The group of factors for presence of lobes.
- (b) The group of factors for depth of the incisions.
- (c) The group of factors for number of lobes.
- (d) The group of factors for extension by which the secondary lobules are developed into lobes.

9. Of these the group of factors for number of lobes consists of at least four interacting factors. The  $F_1$  in these crosses was found to be intermediate and  $F_2$  showed segregation.

10. Races of *Crepis capillaris* with different diameters of capitula were isolated and when crosses were made between such races the diameter of the capitula of  $F_1$  was found to be intermediate between the two parents. The work has not progressed far enough to study the  $F_2$  plants and determine the type of segregation.

11. As far as studied, environment, except moisture, has very little influence on the size of capitula.

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PLATE 42

Fig. 1. Very young stage; cotyledons still persist.

Fig. 2. Early rosette stage.

Fig. 3. Later rosette stage.

Fig. 4. Nearly mature rosette in a family showing a characteristic retrorse rolling of the leaf margins.

Fig. 5. Fully developed rosette, the stage in which measurements of length of radical leaves were taken.



Fig. 1



Fig. 2



Fig. 3



Fig. 4



Fig. 5

PLATE 43

Fig. 1. Fully developed plant of spreading habit, i.e., having many divaricate branches arising from the base of the axis. Fully open capitula shown.

Fig. 2. Nearly mature plant similar to that shown in fig. 1, but of erect habit.

Fig. 3. Mature plant of distinct habit, having no secondary branches arising from the base of the axis.

Fig. 4. Mature plant of spreading habit, but a dwarf in stature.

Fig. 5. Fully open capitula such as were used in taking measurements of diameter.

Fig. 1



Fig. 3



Fig. 2



Fig. 5

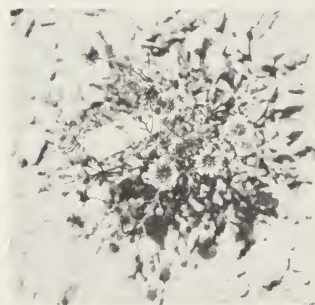


Fig. 4

